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L.H. McMullen, A.J. Thomson and R.V. Quenet

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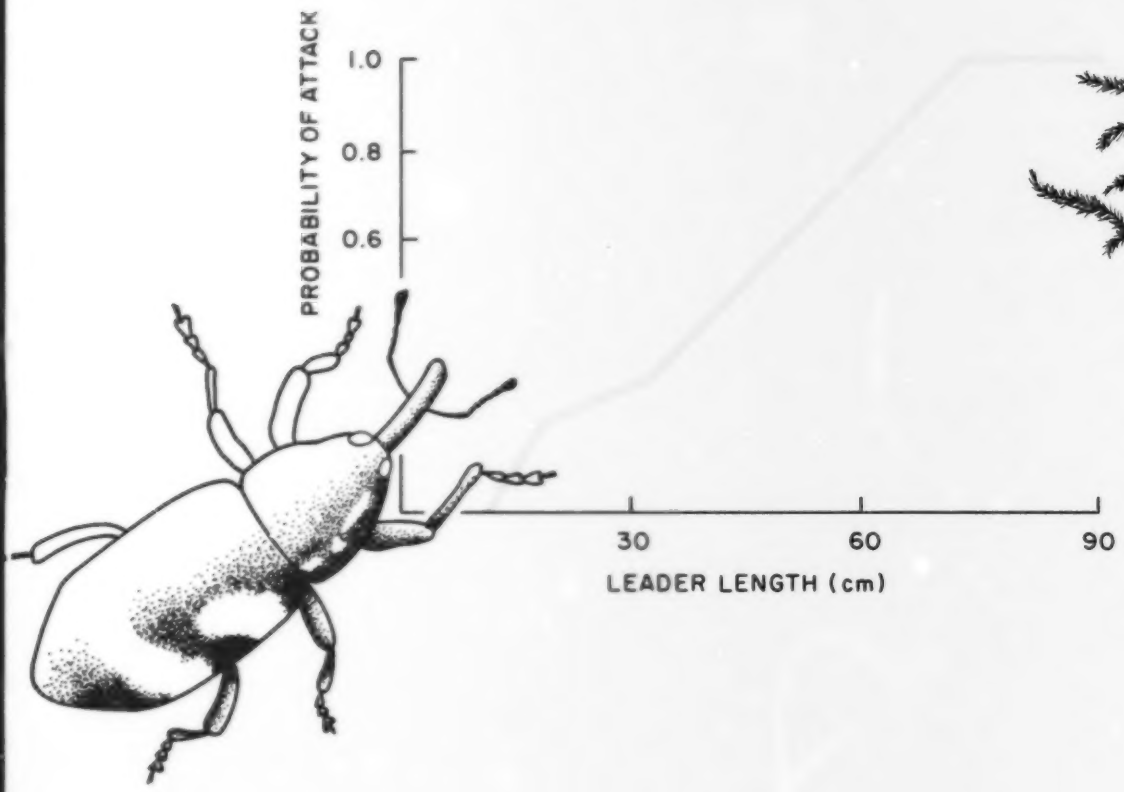

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Contents

Abstract/Résumé 4

Introduction 5

Model Construction 5

- Spatial and temporal scale 5
- Height growth 5
- Growth of weevil-attacked trees 6
- Crown and diameter growth 6
- Tree mortality 7
- Distribution of weevils among height classes 7
- Weevil attack 8
- Weevil reproduction and adult survival 8
- Control options 9

Model Validation 10

Model Behavior 11

Discussion 15

References 16

Appendix 18

Abstract

This report describes a simulation model of spruce weevil-host interaction based on previously published information and the results of a range of studies carried out over a number of years. This model provides the background necessary for understanding the interaction of the spruce weevil and its host, and for examining the relative merits of various control strategies. Effects of chemical control, leader clipping, and interplanting of nonhost trees were studied using the model. Chemical control and leader clipping by themselves are unlikely to be successful, while the silvicultural option (interplanting nonhost trees) appears to be a potentially useful approach to reducing weevil populations.

Résumé

Ce rapport décrit un modèle de simulation de l'interaction entre le charanon de l'épinette et son hôte. Le modèle est fondé sur des renseignements publiés antérieurement et les résultats de diverses études effectuées depuis un certain nombre d'années. Ce modèle fournit les données de base nécessaires pour comprendre cette interaction et pour étudier les avantages relatifs des diverses stratégies de répression. Il a permis d'étudier les effets de la lutte chimique, de la taille des pousses apicales et de la plantation intercalaire d'arbres non hôtes. Les insecticides et la taille des pousses ne devraient vraisemblablement pas donner beaucoup de résultats, mais il semble que le traitement sylvicole (plantation intercalaire d'arbres non hôtes) soit une méthode utile pour réprimer les populations de charanons.

Introduction

Pissodes strobi (Peck) is an economically important native insect including the groups known as white pine weevil, Engelmann spruce weevil and Sitka spruce weevil (the latter two were formerly known as *P. engelmanni* Hopk. and *P. sitchensis* Hopk., respectively) (Smith and Sugden 1969). The main hosts of *P. strobi* are eastern white pine, *Pinus strobus L.*, in eastern North America and spruces, *Picea spp.*, in western North America. It is the most injurious insect pest of Sitka spruce, *P. sitchensis* (Bong.) Carr., regeneration in British Columbia (Silver 1968) and Washington and Oregon (Wright 1960). Repeated attack can render a stand totally unmerchantable (Alfaro 1982).

The insect kills the leaders of trees by feeding gregariously as larvae between the bark and wood. The female weevil typically deposits eggs in the phloem just below the terminal bud of the previous year's leader in May and June. The larvae feed downward in the leader, pupate, and emerge as young adults in August and September (Silver 1968). The adults overwinter in the duff or in the crown (McMullen and Condrashoff 1973). The host responds by replacing the killed leader with laterals which compete for dominance causing crooks, forks and general bushiness. Silver (1968) found that natural mortality factors reduced the beetle population level but were incapable of exerting control. Insecticides could be used to achieve satisfactory control, but this required repeated applications to protect plantations through the critical years.

Clipping of infested leaders and interplanting of nonhost trees offer alternatives to chemical control. Evaluation of these techniques requires detailed understanding of the weevil population dynamics in relation to the host growth patterns. The present report describes relationships of spruce growth and weevil biology which were included in a simulation model developed to investigate control options. Control options were evaluated through the simulation by comparison of indicators such as number of weevils in the stand, tree height, and percent of potential volume.

Model construction

Spatial and temporal scale

Growth and damage were simulated for a plot containing 81 individual trees. This size of model allowed for validation with data taken from 81-tree spacing plots maintained by the British Columbia Forest Service. None of the data derived from the spacing plots was used to establish relationships in the model. All relationships were derived from other experiments and publications, as described herein.

The simulation follows an annual cycle to a maximum of 100 years. Within each year of the simulation, processes are examined in the following sequence:

a) Estimation of potential tree height growth.

b) Estimation of actual growth if the tree was recently attacked.

c) Estimation of tree crown and diameter growth.

d) Estimation of tree mortality due to competition.

e) Assignment of surviving trees to height classes.

f) Distribution of weevils among height classes, and among leaders and competing laterals on the individual trees within the height classes, leading to attack.

g) Destruction of attacked leaders by weevils.

h) Production of new weevils.

Height growth

Mean potential height (HTmp) (m) in relation to age (AGE) and user-defined (see Appendix) site index (SI) (height at age 50) for Sitka spruce was obtained from Eq. 1 (Hegyi *et al.* 1979).

$$HTmp = 1.3783\ (SI)\ (1-e^{0.038\ (AGE)})^{1.9804} \qquad (1)$$

This curve was assumed to be that for a weevil-

free stand. Mean annual potential height increment was obtained from the difference between successive values of the height/age curve (Eq. 1). While average height growth was assumed to follow the site index curve, individual tree growth rates were assumed to be normally distributed; thus a relative growth factor was obtained for each tree by drawing randomly from a normal distribution of mean 0.522 and standard deviation 0.2. Annual potential height increments (leader lengths) of individual trees were determined by weighting the mean height increment by the relative growth factor allotted to the tree. An overall rescaling was carried out on all growth increments to ensure that the average increment followed the site index curve (Eq. 1). The model simulates a spaced managed stand and average spacing is used to define inter-tree distances. The simulation projects both the potential (unattacked) and actual (attacked) tree growth.

Growth of weevil-attacked trees

When a leader has been attacked in the simulation, it is replaced by competing laterals, one of which becomes dominant after a number of years. In the interim, competing laterals can be attacked by the weevil. All trees in the simulation were assumed to recover to a single straight bole, although stem deformities such as forked tops and crooks are common in nature.

The number of laterals competing for dominance on a tree following attack is variable. In a survey of 242 attacked trees done in 1975 at Flora Lake, British Columbia the number of competing laterals varied from one to five following attack and averaged 2.25 (standard deviation = 0.86). The proportions of one to five laterals were 0.18, 0.49, 0.28, 0.03, and 0.02, respectively. Consequently, the number of competing laterals following attack was determined in the model by a five-item probability array.

In the model, competing laterals may be attacked in the model before dominance is asserted, but no additional competing laterals are formed as a result of attack when more than one lateral is present. After a given number of years following attack, assertion of dominance reduces the number of competing laterals to one. The length of this period can be varied, although experience suggests it is about 4 years in nature.

All laterals, initially smaller than the leader, were assumed to approach the potential leader length over a period of two years. In the year of attack, the previous year's leader is replaced by the previous year's lateral. This lateral length is determined as a function of leader length (Eq. 2).

$$\textit{Lateral length} = 1.50876 + 0.469\ \textit{leader length (cm)} \qquad (2)$$

This relationship (r = 0.8635) was determined from measurements of the leader and longest lateral of 50 trees in 1974. Lateral growth in the year of attack, and in the year following attack, is determined in the model as user-defined proportions of potential leader growth. The following year (the second year after attack), the growth returns to its potential. Where competing laterals are present, these are assumed to grow equally.

It was assumed that there was no impact of weevil attack on crown width or dbh growth. These parameters for attacked trees were obtained from the calculations for the potential tree. Volume growth impact occurred in Eq. 6 as a result of reduced height, although Thomson *et al.* (1982) indicate that repeated top damage may reduce the applicability of such equations.

Crown and diameter growth

Relationships for crown width and bole diameter were based on Mitchell (1965, 1969, 1975):

$$CR = 0.5484\ (HT)^{0.75} \qquad (3)$$

where CR is the crown radius (m) projected to the ground and HT is the tree height (m), and

$$CA = \pi CR^2 \qquad (4)$$

where CA is the crown area projection to the ground. DBH (cm) was then obtained from an empirical relationship as

$$DBH = 1.9588\ (2CR)^{0.66}\ (HT - 1.5)^{0.585} \qquad (5)$$

Volume (m^3) is calculated from Eq. 6 (British Columbia Forest Service 1976), and corresponds to gross volume above the stump.

$$\log_{10} VOL = -4.310416 + 1.822840 \log_{10} DBH + 1.057290 \log_{10} HT \quad (6)$$

Tree mortality

Tree mortality occurs as a result of competition which was assumed to be a function of spacing (planting distance) and crown growth. Competition was simulated by crown overlap and consequent reduction of crown area to a specified proportion of that of an open-grown tree below which the tree dies.

Crown overlap (CO) was calculated as the difference between the area available for growth (spacing^2 × number of trees) and area required for open growth (Eqs. 3 and 4). Crown area reduction of a tree (CAR_i) was a function of average crown overlap and the proportion of total crown overlap (CO) attributable to the tree:

$$CAR_i = 0.3 \frac{CO}{n} + 0.7 \frac{CA_i \cdot CO}{CA} \quad (7)$$

where n is the number of live trees.

The effective crown area of the tree (ECAi) and relative effective crown area (DC) were determined as follows:

$$ECA_i = CA_i - CAR_i \quad (8)$$

$$DC = \frac{ECA_i}{CA_i} \quad (9)$$

Tree mortality was assumed to occur when DC fell below 0.1.

After determining mortality, trees were allocated to height classes, with limits at 1.2, 2.1, 3.0, 6.1, 9.1, 12.2 and 15.2 m.

Distribution of weevils among height classes

The algorithm for distributing weevils among trees in different height classes was based on our understanding of weevil behavior (Silver 1968; Gara *et al.* 1971; VanderSar and Borden 1977; Wallace and Sullivan 1985; Alfaro and Borden 1985). Firstly, weevils do not examine every tree in a stand, but respond to the trees in the immediate environment. Therefore, the number of weevils which go to trees in a particular height class will be directly proportional to the proportion of the total trees in the iTH height class (PCT_i).

Secondly, weevils in the laboratory orient preferentially towards larger vertically elongated silhouettes, and in the field they prefer upright longer leaders which generally occur on taller, faster growing trees. The number of weevils going to trees in a particular height class is therefore assumed to be proportional to the position in the cumulative height distribution, i.e., to the average ranking ($CPCT_i + CPCT_{i-1}$)/2, where $CPCT_i$ is the cumulative proportion of trees less than or equal to the upper size limit of the iTH height class.

While the above relationship describes the effect of position in the size distribution, the proportion of weevils going to a height class is also assumed to be proportional to the relative size of the trees, i.e. to (i/i_{50}) where i is the iTH class and i_{50} is the class containing the 50th percentile of the cumulative distribution. Finally, the relative ability of weevils to discriminate the larger size classes from the smaller size classes is assumed proportional to a user-defined discriminability factor (DISC).

Thus the proportion of the weevil population going to a height class ($APPOR_i$) is determined from a weighting factor (WF_i)

$$WF_i = PCT_i \cdot \frac{CPCT_i + CPCT_{i-1}}{2} \cdot \left(\frac{i}{i_{50}}\right)^{DISC} \quad (10)$$

and

$$APPOR_i = \frac{WF_i}{\sum_{i=1}^{8} WF_i} \quad (11)$$

This procedure is consistent with known weevil behavior and allows the user to vary the effects by modifying a single variable (DISC).

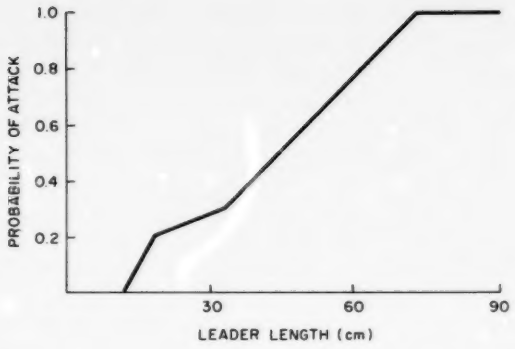

Figure 1. Probability of attack in relation to leader length, based on the data of Silver (1968).

Weevil attack

Following allocation of weevils to height classes, each tree in a height class is examined separately to determine if it is attacked. Attack on the tree occurs as a probability function of leader length (Figure 1). This relationship was based on the leader length and attack data of Silver (1968); these data were collected between 1960 and 1963 and provided information on 1185 leaders of which 159 were attacked. Kolmogorov-Smirnov tests (Sokal and Rohlf 1969) indicated that leader length was a more important factor in attack probability than tree height. In the model, attack on a tree is determined by comparing a random number with the expected probability of attack.

Many years of field studies (Harris *et al.* 1968; McMullen 1976a; McMullen and Condrashoff 1973) led to the conclusion that for trees over 12 m tall, the probability of attack is inversely related to tree height. Therefore, a maximum probability of attack as a function of tree height (Figure 2) is incorporated in the simulation in a manner which reflects this experience. Thus, although weevils may orient to those trees in a stand which are taller than their neighbors, some unknown feature related to the absolute height of the trees may limit actual attack on the trees.

A limit to the number of attacks in a height class is imposed, based on the assumption of a random allocation of weevils over the trees in the class. The maximum proportion of trees that may be attacked in the class (MPTA) was therefore determined from the probability of one or more weevils going to each tree given the number of trees in the class (ICLASS) and the number of weevils (PER) in the height class. Thus

$$MPTA = 1 - \left(\frac{1}{ICLASS}\right)^{PER} \qquad (12)$$

Weevil reproduction and adult survival

The weevil population is initiated for each run by the introduction of one or more females in a specified year. Eggs and larvae are not simulated explicity for the following reason. In an attacked leader, the larvae form a "feeding ring" around the circumference of the leader. The ring of feeding larvae works its way down the leader (Wallace and Sullivan 1985). Brood production is therefore much more closely related to leader diameter than to number of attacks or number of eggs laid. Leader diameter is highly correlated with leader length; thus, attacked leaders produce young weevils (YW) according to a user-defined function of leader length,

$$YW = a + b\,(leader\ length\ (\text{cm})) \qquad (13)$$

where a is the y intercept and b is the slope. Both a and b are user-defined values. Examination of emergence holes and leader lengths in 1974 sug-

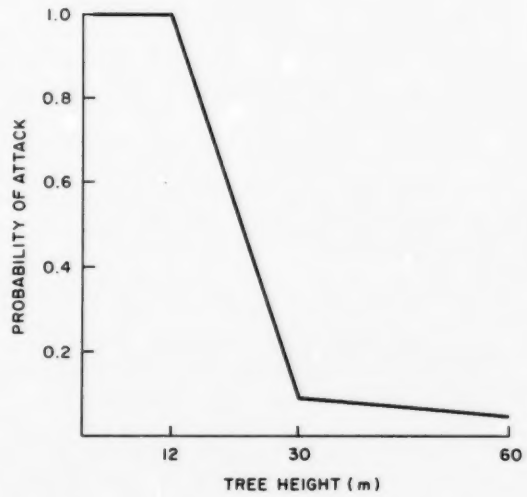

Figure 2. Probability of attack in relation to tree height.

gested that 0.6753 and 0.2338 would be approximate values for a and b respectively.

This level of productivity was modified by weather. McMullen (1976b) reported 888 degree-days above 7.2°C (1600 degree-days above 45°F) for brood development. Oviposition occurs during May and June, thus 100% emergence of all brood would require 888 degree-days after June 30. Unpublished studies of heat accumulation during the oviposition period in May and June of 1970 and 1975, together with the published study, indicated that 1167 degree-days would be required during May through September for emergence of all eggs deposited while with fewer than 888 degree days there is no emergence. For heat unit totals between these extremes, 888 and 1167 degree-days for 0 and 100%, emergence was interpolated in relation to the occurrence of heat units as in Figure 3. Year-to-year variability of heat accumulation in the model is a user-defined option.

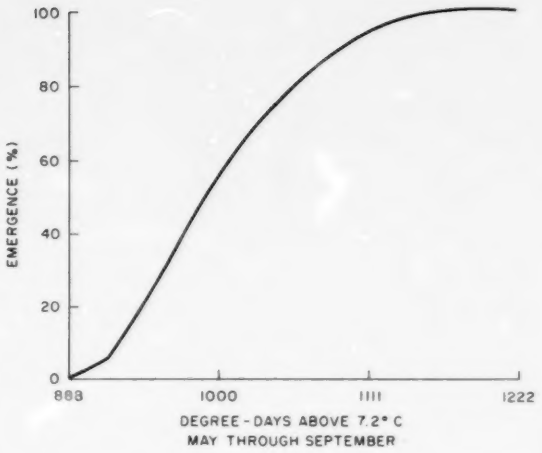

Figure 3. Percent weevil emergence in relation to heat unit accumulation from the beginning of May through September.

It was assumed that no mortality of emerged beetles occurred in the year of emergence. However, in subsequent years a user-defined proportion of the adult weevils die. Adults have been observed to live as long as 5 years (McMullen and Condrashoff 1973).

Control options

Approaches to control are simulated in the model by influencing the population level at different stages in the annual cycle. The influence is either through direct mortality of adults, reduction of the number of weevils emerging from attacked leaders, or by influencing the behavior of adults so that some do not attack host trees.

"Chemical" control is achieved by killing a user-defined proportion of the weevil population before oviposition occurs at the beginning of the annual cycle. This can be carried out in any of one to five different years and the total population is affected each year control is applied. No attempt is made to simulate the complexities of residual toxicity required to contend with the long periods over which oviposition activity takes place (Silver 1968).

Control through "leader clipping" to destroy developing brood is simulated by removal of a user-defined proportion of attacked leaders, reducing the number of young adults that enter the population the following year but with no impact on the old adults surviving from previous years. The effects of clipping unattacked leaders, the increasing difficulty of identifying and removal of infested leaders as stand height increases, or the removal of superfluous laterals to reduce forked tops are not included.

The use of a nurse crop to alleviate damage has been suggested (Berry and Stiell 1976). However, shading by the nurse crop then reduces the spruce growth. An alternative is considered in the model. As discussed earlier, weevil distribution is biased towards the taller height classes in a stand. We therefore hypothesized that interplanted fast-growing nonhost trees (including deciduous trees) might draw off the weevils from the host trees. These nonhost trees could be of a sufficiently low density and slenderness of silhouette that adverse effects on the spruce would be negligible. In the model, therefore, there is the option of replacing host trees with nonhost trees which have a user-defined growth rate different from that of the hosts. By manipulation of the discriminability function described earlier, the degree of selection by weevils of the faster growing nonhost trees can be varied. It is assumed that once weevils have been attracted to these nonhost trees, they disperse out of the stand.

The nonhost trees can be removed once the critical period for weevil attack has passed.

Biological control options are not considered explicitly; at present no direct method of assessing the effect of a reduction of brood productivity over the life of the infestation, equivalent to enhancement of the effect of parasites and predators or any other causes of brood mortality, is available in the model. However, manipulation of the number of weevils per leader or the reduction of emergence due to weather (degree-days) provides an indirect approach to evaluation of such options.

Model validation

As indicated in the description of the construction of the model, 81-tree (9 × 9) spacing trials which have been infested with spruce weevil were examined annually to determine the percentage of trees attacked each year. Spacings in these trials were in English units. Two replicates of each of three spacings were examined and compared with model output at the median spacing (12 feet × 12 feet) (Figure 4). The pattern of attack with time indicated in Figure 4 also agrees closely with that reported by Alfaro (1982).

The model underestimates the rapidity of onset of the infestation, and in turn shows peak damage somewhat later than in the field. However, by age 20, as indicated by accumulation of the annual percentage of trees attacked, the estimate of damage provided by the model is within the range of that observed in the field (Figure 5). Overhulser *et al.* (1972) suggest that weevil emergence may be greater on trees attacked for the first time than on those that have previously been attacked. The model does not include this phenomenon, and this could explain the early differences between the field data and the model.

Orientation of weevils toward taller trees is a key feature of the biology included in the model. This behavior is exploited in the hypothetical control option using interplanted nonhost trees. Influence of tree height and the effects of flushing of deciduous trees on beetle flight were tested in the following experiment. Weevils were allowed to fly from a breast-high post at the center of forest openings surrounded by trees of varying average height, and the heights to which

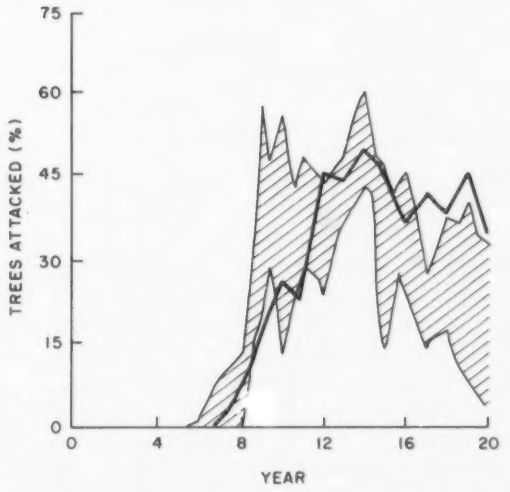

Figure 4. Comparison of annual attack rates in six spacing plots (two at each spacing regime) with the estimate provided by the model at the median spacing. The shaded area illustrates the range of attack rates in the six plots, while the solid line shows the model prediction.

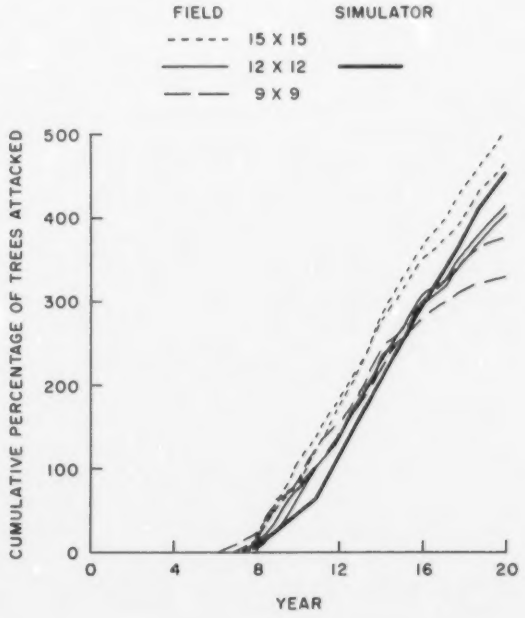

Figure 5. Cumulative annual percent attack rates in six spacing plots compared with the estimate provided by the model at the median spacing. The spacings are given in feet. The heavy line shows the result of the simulation.

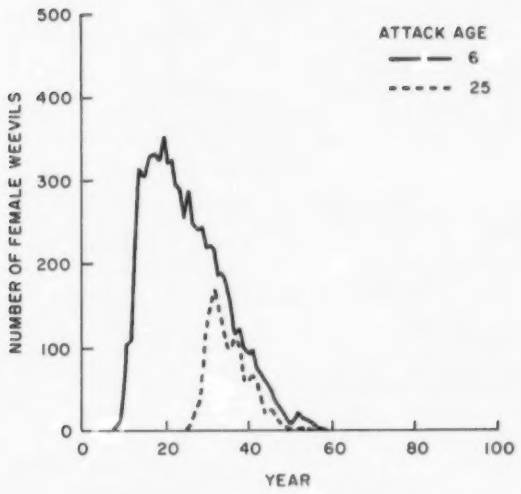

Figure 6. Number of female weevils following early and late introductions into the stand.

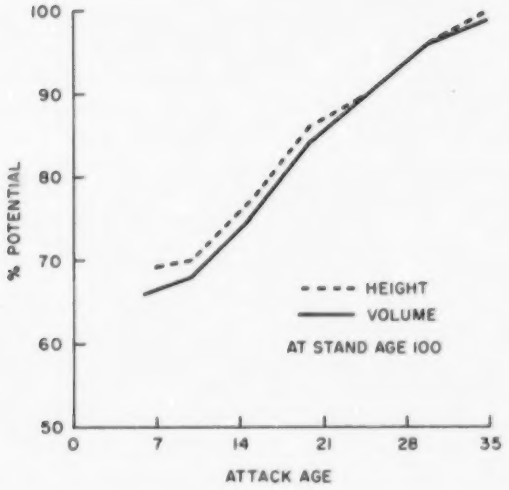

Figure 7. Percent potential volume and height at stand age 100 in relation to time of introduction (attack age) of weevils into the stand.

the weevils flew were recorded. All stands contained Sitka spruce, but one stand included a significant deciduous component. The height to which the weevils flew was directly correlated with the height of the surrounding trees (Table 1). Flushing of the surrounding trees influenced the height of flight. Our algorithm for distributing weevils and the hypothetical control using nonhost trees is consistent with these observations.

Table 1. Flight height of *P. strobi* adults in relation to the condition of the surrounding stand

Average Stand Height (m)	Flush Condition (if deciduous)	Approximate Diameter of Opening (m)	Average Flight Height (m)
1.0	—	10	3.1 a+
8.3	—	11	5.5 bc
10.2†	Partial	16	4.6 ab
10.2†	Full	16	7.3 cd
33.1	—	23	9.1 d

+ Means followed by same letter not significantly different (P. = .05) Duncans new multiple comparison test.

† These data from the same stand before and after full flush.

Model behavior

The model is a stochastic simulation of spruce weevil population dynamics in relation to Sitka spruce growth, and depends on generation of random numbers. An option for varying the seed of the random number generator is included, but the runs for the following model behavior are for the same initial seed. Varying the seed results in slight quantitative changes in performance but does not influence the qualitative responses.

The time at which weevils are introduced into the stand can be varied, resulting in marked changes in the weevil population (Figure 6). Reduction in potential height and volume resulting from changes in the time of introduction are shown in Figure 7. These results demonstrate that control of the insect must be achieved early in the stand history to reduce damage.

Manipulation of the survival of adults after the first year altered the number of weevils active at any time (Figure 8). However, the effect on damage was minimal (Figure 9). In the model, more weevils than suitable leaders are present during the peak population years. Consequently a considerable reduction of the population level is necessary to create an impact on the damage. The fact that in a heavily infested stand more

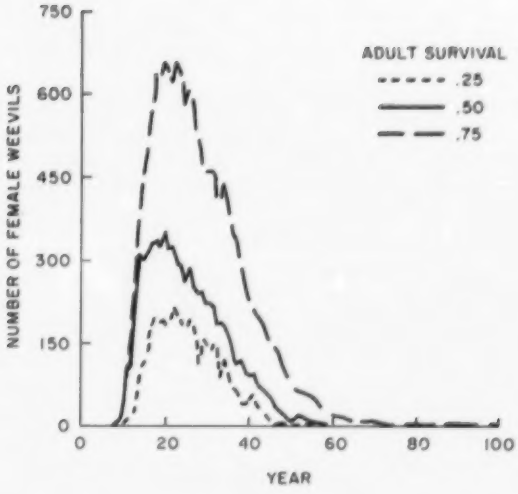

Figure 8. Number of female weevils resulting from different annual adult survival rates.

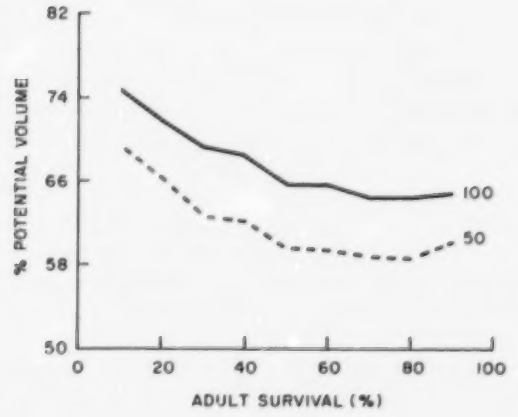

Figure 9. Effect of annual adult survival rates on volume at ages 50 and 100 years.

than one female (sometimes 10 or more) attacks the same leader suggests that the model is simulating the field situation in this respect. Since survival of approximately 0.5 is indicated by the data of McMullen and Condrashoff (1973), this level was generally used.

Effectiveness of different chemical control strategies can be evaluated. For example, the responses of the population to a single application or repeated applications of insecticide producing 99% mortality are shown in Figure 10. The influence of insecticide efficiency (i.e., different mortality levels) on the reduction of damage, in the case of repeated application, is shown in Figure 11. These results suggest that any successful control effort must be thorough and carried out over several years.

The effect of intensive leader clipping to prevent brood production reduces populations of weevils (Figure 12) but has relatively little effect on damage (Figure 13). This is because the number of infested leaders missed (assumed to be 5% in Figures 12 and 13) produce enough young adults, which, together with old adults, can attack most of the suitable leaders. A comparison of leader clipping and chemical control is shown in Figures 14 and 15. The difference is due to the

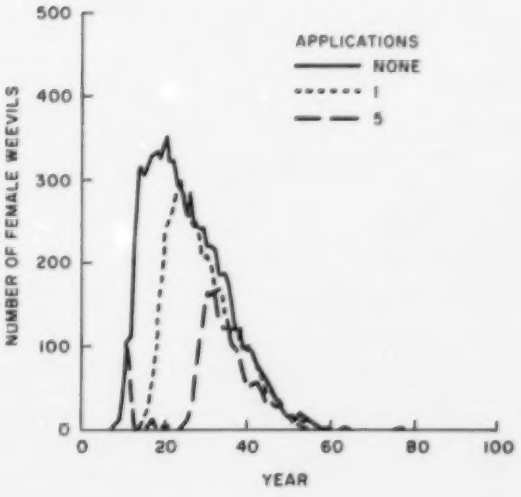

Figure 10. Response of the female weevil population to single and repeated applications of a 99% effective insecticide. A single application at age 12 is compared with five applications at 3-year intervals starting at age 12.

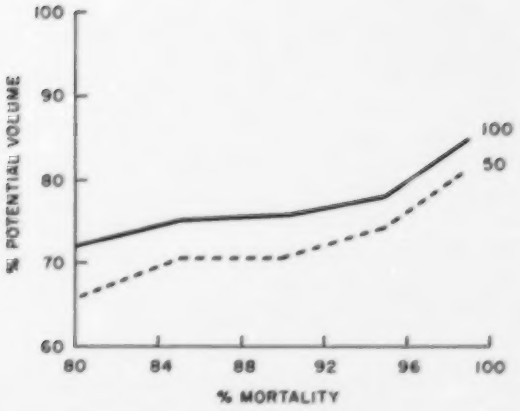

Figure 11. Effect of insecticide efficiency on the reduction of weevil damage after five treatments at 3-year intervals. Damage is evaluated from the percentage of the potential volume at ages 50 and 100.

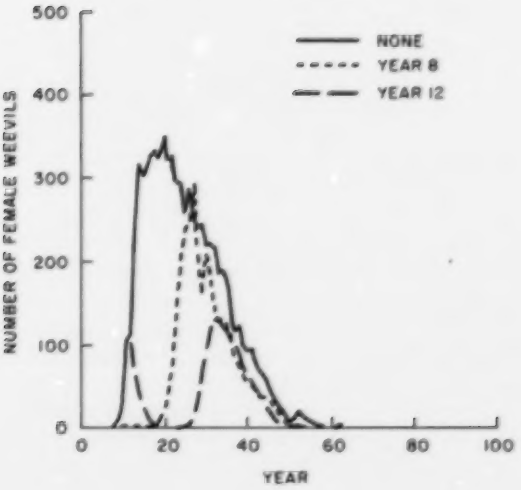

Figure 12. Response of female weevil population to different leader clipping strategies with 95% efficiency. The two clipping strategies begin at ages 8 and 12, and each is applied in 10 successive years.

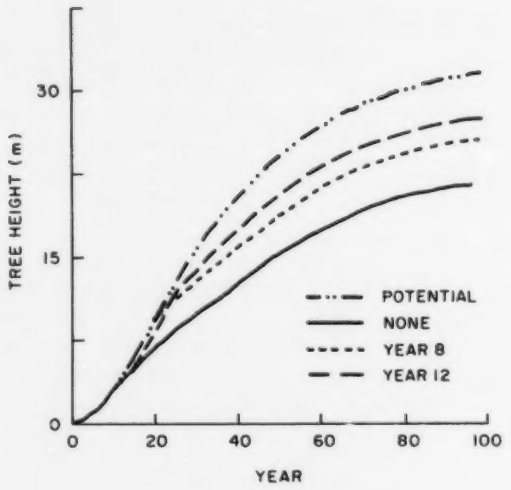

Figure 13. Effect of intensive leader clipping control strategies on tree height. Potential height is compared with the height attained if no control is applied. Leader clippings begin at year 8 or year 12 and continue for 10 successive years.

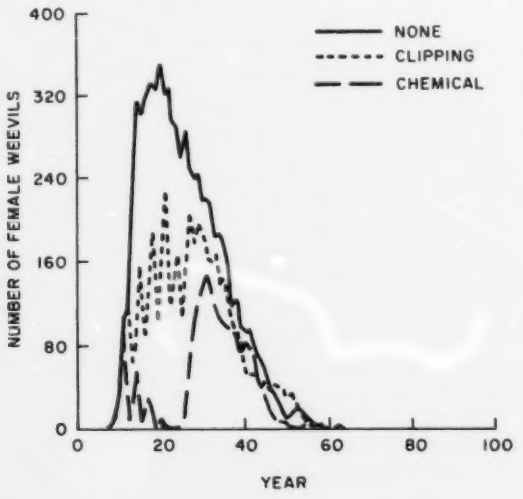

Figure 14. Comparison of equivalent leader clipping and chemical control strategies of 95% efficiency, on the population of female weevils. Five applications of chemicals at 3-year intervals are compared with five leader clippings at 3-year intervals, beginning at year 12.

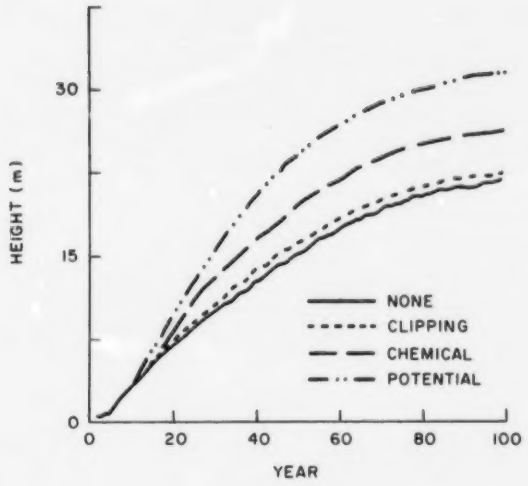

Figure 15. Reduction of damage by chemical and leader clipping control strategies used in Figure 14.

fact that the chemical control is directed against all adults whereas that of leader clipping is directed only against the emerging young adults.

The results of manipulation of population survival to reflect biological control options (Figure 16) suggests that the number of weevils produced per leader would have to be reduced to less than two before a significant reduction in damage would occur. If one assumes that four females per leader is a conservative estimate of average productivity, then mortality factors operating in the leader would have to reduce that productivity over 50%.

A nonhost growth rate approximately 1.5 times that of the host, with the nonhosts removed at stand age 35, was assumed. The effect of different numbers of nonhost trees and different discriminability factors is shown in Figure 17. The results suggest that if the weevils can discriminate the tall nonhost trees well enough they could be directed away from the host trees, using a nonhost density sufficiently low that there would be little adverse effect on the growth of the spruce.

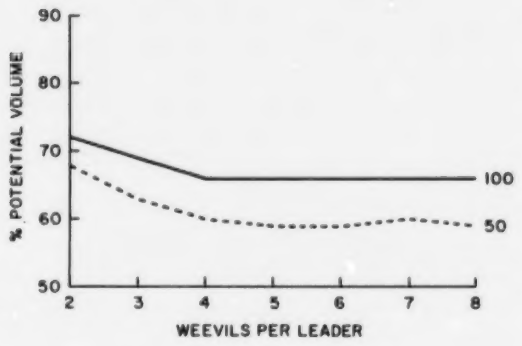

Figure 16. Percent potential volume at ages 50 at 100 in response to number of weevils produced per leader.

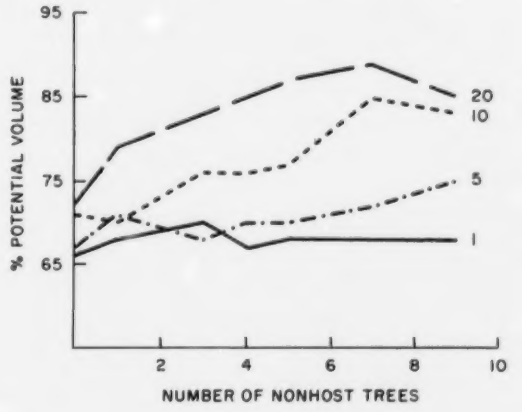

Figure 17. Percent potential volume response to different discriminability factors and numbers of nonhost trees, with nonhost trees removed at stand age 35. Discriminability factors of 1, 5, 10 and 20 were used.

Discussion

In developing the simulation model of Sitka spruce growth and spruce weevil population dynamics and impact, some features were incorporated explicitly while others were implicit. The major explicit features included variability in tree growth rates and weevil response to these through orientation to taller silhouettes, and attack proportional to leader length. The longevity of the adults was also included, as was the formation of a "feeding ring" by the larvae, and the effect of weather on survival.

Tree spatial pattern, weevil oviposition rates, and larval development and survival were implicit. As the model was based on allocation of trees to height classes, with weevils being apportioned among these classes, the individual tree locations were not required. Formation of a feeding ring by the larvae made brood survival much more dependent on leader size than on oviposition rates and larval survival rates; thus the number of progeny was determined solely from the length of an attacked leader, and the number of attacks on the leader was not explicitly determined. The oviposition period in the spring is known to be prolonged (Wallace and Sullivan 1985). This results in field populations in which a wide range of developmental stages and tree symptoms may be present at any one time. While this temporal variability of developmental stage is not made explicit in the model, it must be considered in interpreting the performance of different control measures.

Control methods in the model are of three main types: those which reduce the number of adults, those which reduce the production of new adults per attacked leader, and those which reduce the number of attacked leaders. A user-defined proportion of the adult weevils may be removed from the population in specified years by the option titled "chemical control." Only the year of implementation of the control measure and its effectiveness are specified. On account of the variability of developmental rates, these methods should be interpreted as either (1) frequent enough applications during the season to achieve the desired effect, or (2) sufficiently early application of a control measure with a long-term residual effect to achieve the specified reduction of population. Similarly, tree symptoms on which leader clipping operations are based may develop over a protracted period; several clipping operations may be required in a year to achieve the desired efficiency. In practice, it is difficult to ensure that a high proportion of attacked leaders are removed, especially as the trees grow taller and crown closure occurs.

Alternative control measures may be simulated indirectly through manipulation of the annual adult survival rate, or through the degree-day effect on brood production. A hypothetical control method based on interplanting of nonhost trees was proposed, based on the orientation behavior towards taller trees. Efficiency of this method varied with the assumed ability of the weevils to discriminate taller trees. Implicit in this hypothetical method is the assumption that once beetles are attracted to the taller nonhost trees, their subsequent flight is a disperal out of the stand. Subsequent flight from the nonhost trees would lead to loss of weevils from the stand. This would be appropriate for small plantations surrounded by nonhost trees, and is consistent with field observations, but it may not be appropriate in more extensive plantations. Additional information on weevil dispersal is required to evaluate this possibility.

Control measures directed against the larval stages are hindered by the normal larval behavior: as the larval "feeding ring" works its way down the leader, larvae competitively excluded from this feeding ring suffer very high rates of starvation mortality. Failure of some control strategies relates to the fact that they mainly kill larvae which would otherwise die from this competitive feeding behaviour. Impact of predators and parasites is also reduced if they attack these excluded larvae. Parasitoids or predators have a better opportunity to exert control if they are active against the weevil pupae (Alfaro and Borden 1980).

Effectiveness of control measures was in all cases evaluated by comparison of heights and volumes with the potential growth. In practice, however, weevil effects on tree quality (e.g., forks, crooks, creases, buried leaders) may be at least as important as volume reduction. Impacts presented should therefore be interpreted in a purely relative sense.

In summary, therefore, long-term attack rates es-

timated by the model are comparable to those observed in spacing trials infested by the weevil as well as to those reported by Alfaro (1982). While intensive leader clipping and chemical control programs may delay the onset of damage, they do not achieve significant reduction of damage in the long term. Any beneficial effects observed assume high success rates which would be difficult to achieve in the field on account of (1) the long time span over which adults and larvae are active, (2) the low mortality rates of the adult weevils, (3) the high reproductive potential, and (4) on the feeding behavior of the larvae.

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Appendix

Table A.1. Control file for a single run of the spruce weevil model. The first 20 characters of each record are used to comment on the input variable, while all records following the name of the output file are used for general comments.

Attack Age	: 6
INRAN (Min=20) INTOP	: 20, 0
# of Female Weevils	: 1
Site Index	: 30
Simulation Period	: 100
Spacing (m)	: 2.74
First, Second	: .5, .75
Wev/Led — Int,Slope	: 4., 0.
Survival	: .5
Degree Days	: 2100., 2100., 2100., 2100., 2100., 2100., 2100., 2100., 2100., 2100.
Max. # of Laterals	: 5
Prob of each ffLats	: .18, .48, .28, .03, .02
#Years to Dominance	: 4
Discriminability	: 1.
#Chem Controls	: 0
Age at each Applic.	: 0
%Kill at each Applic.	: 0
# of Nonhosts	: 0
Nonhosts start age	: 0
Nonhost yr of cut	: 25
Nonhost age, Ht (4)	: 0., 0., 5., 4., 15., 14., 35., 24.
# Leader Clip Apps	: 0
Age at each Applic.	: 0
%Infested Remove/Ap	: 0
Output File Name	: MCM7RUN.M
C	
C File Name	: MCM7.MOD
C Purpose	: Basic input file for weevil model

Table A.2. Description of the input variables in the simulation control file.

Attack Age	: Stand age at which weevils are entered into the model.
INRAN (min=20),INTOP	: Selection of random number generator seed, selection of intermediate output (0 = No, 1 = yes).
# of Female Weevils	: Number of weevils entered at the above attack age.
Site Index	: Height at age 50.
Simulation Period	: Number of years for simulation to run.
Spacing	: Distance between trees (m).
First, Second	: Proportion of normal leader growth that competing laterals grow in the year of and in the year following attack.
Wev/Led — Int,Slope	: Intercept and slope of a line giving the number of weevils produced per leader.
Survival	: Survival of adults after the first year.
Degree-Days (10)	: Number of degree-days above 7.2 degrees from May through September (890 to 1167) for each of 10 years. Values larger than 1167 are used to ensure no adverse weather effects on survival.
Max # of Laterals	: Number of laterals (1 to 5) competing for dominance following attack.
Prob. of each # Lats	: Probability of one to the maximum number of laterals occurring.
# Years to Dominance	: Number of years after attack that one leader assumes dominance.
Discriminability	: Factor increasing the number of weevils going to taller trees.
# Chemical Controls	: Number of years (0 to 5) in which weevils are killed before oviposition (attack).
Age at each Applic.	: Stand age at which the above controls are to be applied.
% Kill at each Applic.	: Percent mortality in each of the above control years.
# of Non-hosts	: Number of host trees that are replaced by nonhost trees.
Nonhost start age	: Age of nonhost trees when simulation starts.
Nonhost yr. of cut	: Stand age when nonhost trees are removed.
Nonhost Age, Ht (4)	: Growth rate of nonhost trees; four pairs of age and height.
# Leader Clip App	: Number of years (0 to 10) in which infested leaders are removed before emergence of young adults.
Age at each Applic.	: Stand age at which each of the above clipping procedures are to be carried out.
% Infested Remove/app	: Percentage of the infested leaders that are removed in all years of application.
Output File Name	: Name of the file to which output occurs.

Table A.3. Variables included in the normal model output which is in the form of a 17-variable table with the values repeated each year.

Stand age
Number of female weevils
Number of new female weevils
Number of old female weevils
Number of leaders
Number of leaders attacked
Number of trees attacked
Cumulative attacks on trees
Cumulative attacks on leaders
Percentage of leaders attacked
Percentage of trees attacked
Actual mean tree height (m)
Potential mean tree height (m)
Volume (m^3) of the stand (actual)
Volume (m^3) of the stand (potential)
Number of living trees in stand
Height increment (cm).